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Glacial-interglacial excursion in the concentration of atmospheric CO_2: effect in the $^{13}C/^{12}C$ ratio in wood cellulose

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ABSTRACT

Stable carbon isotope ratios ($^{13}C/^{12}C$) of cellulose extracted from wood belonging to the last glacial-maximum period (20 ± 2k yr) is on the average 4‰ higher than that for the corresponding ratios from the recent interglacial age, and could not be the result of any changes in humidity or temperature alone. This temporal variation of $\delta^{13}C$ in wood cellulose corresponds chronologically to the reduced concentration of atmospheric CO_2 measured in glacial ice cores, thus providing the first direct evidence of the effect of reduced atmospheric CO_2 concentration on land biota. The higher $\delta^{13}C$ in wood cellulose and the manner in which it varies with time could be explained if, in addition to causes introduced by a changing ocean chemistry during glacial time, there is an additional carbon reservoir created by vegetation flourishing in the newly exposed land surfaces accompanying a lowering of the sea level.

1. Introduction

Carbon dioxide forms an important component of the atmospheric constituents principally through its role in terrestrial productivity and oceanic chemistry and its ability to act as a "greenhouse" gas. Therefore, there is growing concern in the past few decades over its steady increase, due mainly to anthropogenic factors. There have been suggestions that there is a link between the rising CO_2 levels in the atmosphere on the one hand and the observed global temperature rise that has been reported on the other (Manabe and Wetherald, 1980; CDAC, 1983; Hansen et al., 1981; Woodwell et al., 1983). Evidence also seems to exist that photosynthesis and related plant activity may already be responding to such an increased level of atmospheric CO_2 (Lemon, 1983; LaMarche Jr. et al., 1984). Thus, a knowledge of past CO_2 variations in the atmosphere and its accompanying isotopic variation assumes great importance and may be vital in any global climate as well as carbon cycle modelling studies.

Recent trend in the concentration of atmospheric CO_2 is known from direct measurements which are available for the past few decades (Keeling et al., 1979, 1984; Mook et al., 1983). The possibility of obtaining direct information regarding CO_2 fluctuations in the past from air trapped in polar ice cores has provided a fresh impetus to carbon dioxide research (Neftel et al., 1985; Raynaud and Barnola, 1985; Barnola et al., 1987; Sigenthaler and Oeschger, 1987; Neftel et al., 1988; Stauffer et al., 1984). Studies utilizing this technique reveal interesting information related to CO_2 variations over time scales of centuries or even millienia. For example, these results point to an increase of almost 23% in the atmospheric CO_2 concentration between 1750 and the present and, more strikingly, document a substantially lower atmospheric CO_2 level during the concluding phase of the last glacial period, between 20k years and 16k years before present. While a CO_2 concentration record in ice cores from Greenland indicate concentrations as low as 180 ppm during the last glacial maxima, it is generally believed that, given all the uncertainties

described above, the glacial atmospheric concentration of atmospheric CO_2 was about 200 ppm as compared to 275 ppm at the termination of the last glacial and onset of the interglacial (Broecker and Peng, 1986). Moreover, as indicated by the work of Stauffer et al. (1984), there is also evidence from the Greenland ice core that this shift in CO_2 level between the glacial and the interglacial periods could have been quite dramatic, occurring in as little as a few centuries. Such large scale changes in atmospheric CO_2 levels can be expected to leave an imprint on the $^{13}C/^{12}C$ of free atmospheric CO_2 and the biosphere. While more precise measurements of $^{13}C/^{12}C$ of CO_2 trapped in glacial ice alone might reveal if the $^{13}C/^{12}C$ of atmospheric CO_2 of that period shows the expected deviation, one obvious approach is to analyse the $^{13}C/^{12}C$ of cellulose extracted from wood belonging to the glacial and interglacial periods. This is reasonable since there is much evidence that the $^{13}C/^{12}C$ measurements on cellulose from tree rings reflect to various degree of faithfulness the $\delta^{13}C$ of atmospheric CO_2 (Peng and Freyer, 1986; Freyer, 1986; Leavitt and Long, 1986; Freyer and Belacy, 1983).

2. Material and method

Ancient wood samples that were dated by the radiocarbon dating method as well as modern wood samples were chemically treated to separate the cellulose fraction. The treatment basically consists of the removal of lipids and resins using benzene-methanol mixtures, softening by boiling in water and oxidation using sodium chlorate. While the modern wood samples invariably required up to four oxidation steps, many of the ancient ones were subjected to only two so as not to destroy the sample completely. The two oxidation steps provided sufficient cellulose for analysis. Dry cellulose extracts were combusted in evacuated, sealed vycor tubes at 900°C for 3 hours in the presence of pre-cleaned cupric oxide and the carbon dioxide produced in the combustion analyzed in a Nier type ratio mass-spectrometer (McKinney et al., 1950). The $^{13}C/^{12}C$ ratio is reported in the usual per mil notation, where

$$\delta^{13}C = \frac{(^{13}C/^{12}C)_{sample}}{(^{13}C/^{12}C)_{standard}} - 1 \times 10^3.$$

Overall analytical reproducibility was 0.1‰. Appendix 1 contains all the available details of

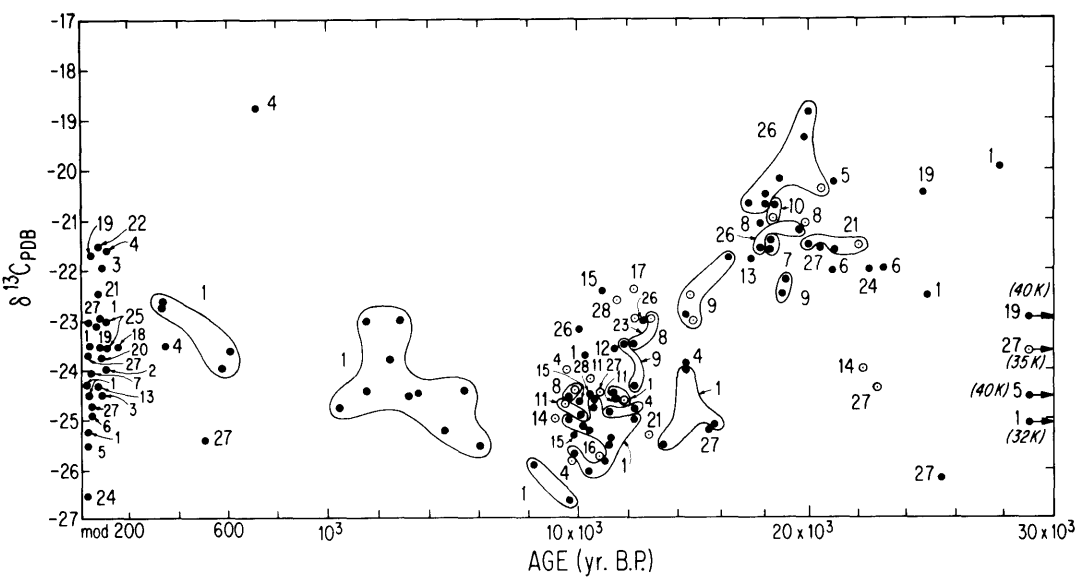

Fig. 1. $\delta^{13}C$ of wood cellulose as a function of time. Circled samples were analyzed by Yapp and Epstein (1977). "Modern" samples are younger than 1850 A.D. Sample locations are: Alaska (1), Africa (2), Australia (3), California (4), Chile (5), Georgia (6), Illinois (7), Indiana (8), Iowa (9), Kentucky (10), Michigan (11), Minnesota (12), Missouri (13), Nebraska (14), N. Dakota (15), New Jersey (16), New Mexico (17), New York (18), New Zealand (19), Nicaragua (20), Ohio (21), S. Africa (22), S. Dakota (23), W. Africa (24), Texas (25), Utah (26), Washington (27), Wisconsin (28).

sample locations, their ages and the $\delta^{13}C$ values. Modern samples refer to those younger than 100 years.

3. Cellulose $\delta^{13}C$ versus CO_2 concentration in the atmosphere

The $\delta^{13}C$ values of cellulose extracted from the ancient and modern wood samples collected from various sites as a function of their age is also given in Fig. 1. In addition to the data obtained by us we have also included those reported earlier by Yapp and Epstein (1977). Since the modern samples, being younger than 100 years, may also incorporate the CO_2 released by anthropogenic factors, a correction has been applied to all these modern samples. The correction involved the assumption that there has been a decrease of 1‰ in the $\delta^{13}C$ of atmospheric CO_2 between 1850 and about 1975 caused by the addition of fossil fuel derived CO_2 to the atmosphere. Thus the correction would be anywhere between 0 and 1‰ depending on whether the modern sample has grown between 1850–1855 or during the last few years. Such a correction of 0–1‰ is not entirely arbitrary in that while anthropogenic CO_2 increase in the atmosphere over the last century may have been found to be nearly exponential, the resulting effect in tree rings appear to average around 1‰ (Peng et al., 1983; Peng and Freyer, 1986). We have analyzed two long tree ring sequences, a bristlecone pine from White Mountains California covering the past 1000 years and a Juniper from the Sinai region in Egypt (Epstein and Krishnamurthy, 1990). These two sequences from widely separated but representing free atmosphere conditions show identical $^{13}C/^{12}C$ variations and also support an anthropogenic CO_2 effect of 1‰. Fredli et al. (1986) have reported the $\delta^{13}C$ of air trapped in polar ice for the same time period which suggests an overall 1‰ depletion for the same time period. In Fig. 2 we plot those samples for which there is

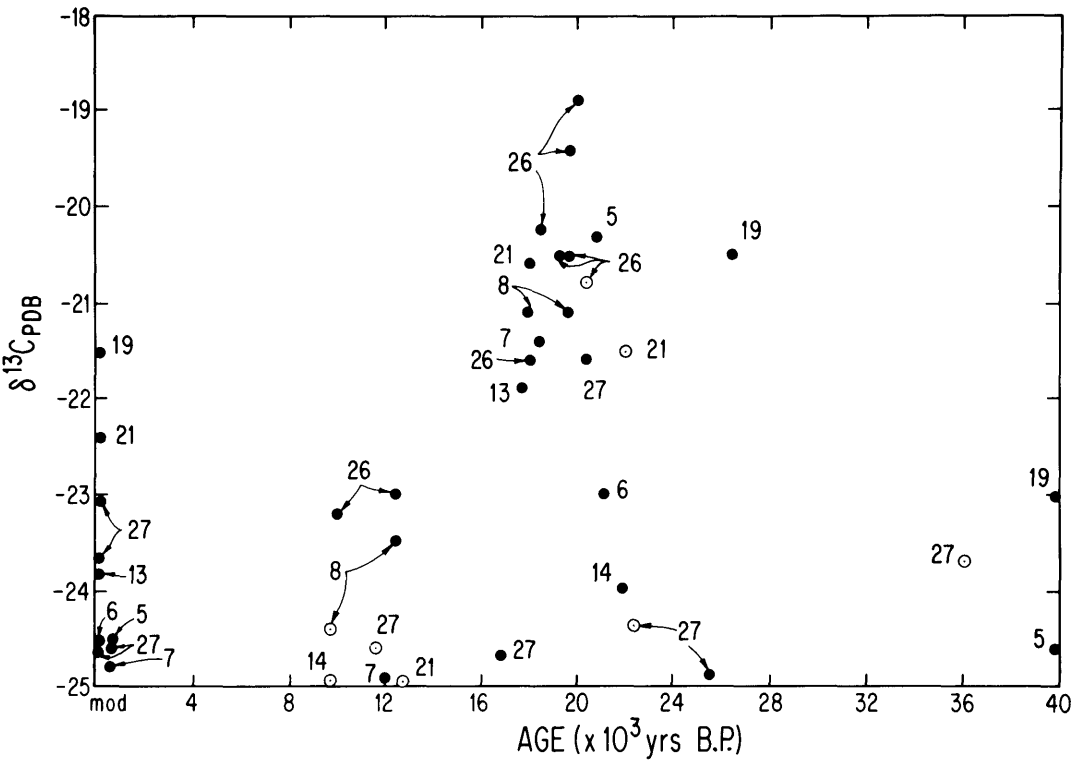

Fig. 2. $\delta^{13}C$ of cellulose of wood sampled from the same general location plotted as a function of time. All other details as in Fig. 1.

a modern and old sample in the same general location. This plot is to illustrate the difference in the $\delta^{13}C$ between the two time ranges. In Fig. 3 we have plotted the mean $\delta^{13}C$ representing various age brackets together with their standard deviation. Also shown in this figure is the record of variation in the concentration of atmospheric CO_2 as obtained from the analysis of air bubbles trapped in an Antarctic ice core by Barnola et al. (1987).

The most interesting feature evident from our analysis shown in Fig. 1 is the clear distinction in the $\delta^{13}C$ values of samples representing the last glacial maximum and beginning of the present interglacial period (CLIMAP, 1976). Samples covering the time bracket 22k–17k years have a $\delta^{13}C$ value of $-21 \pm 1‰$ while those in the time bracket 12k–9k years have a value of $-25 \pm 0.8‰$. A shift in $\delta^{13}C$ of this nature was noted by Yapp and Epstein (1977) but the data were too few to be statistically significant. The present study not only encompasses a much larger number of samples but the magnitude of the shift is also greater than could be attributed to climatic variable such as temperature or humidity alone. For example, Stuiver and Braziunaus (1987) reported a significant latitude effect in the $\delta^{13}C$ analysis of North American trees. They attributed this effect to a humidity factor with a coefficient of $-0.06 \pm 0.01‰$/per cent relative humidity. A shift of 4‰ in the $\delta^{13}C$ of glacial samples observed by us therefore would mean a lowering of relative humidity by 66%. We have no basis to evaluate this unlikely possibility. The $\delta^{13}C$ of modern samples exhibit a large scatter with a mean value of $-24.1 \pm 1.1‰$, especially the three samples in locations 19, 22, and 4 have $\delta^{13}C$ values between -21.5 and $-22.0‰$, hence somewhat similar to those belonging to the terminal glacial period. Of these sample locations, 22 and 4 grew in a dry climate, namely the relatively dry regions of South Africa, California and Australia, respectively, while the sample 19 comes from an area with relatively high precipitation, namely New Zealand. One would have expected the $\delta^{13}C$ of the latter sample 19 to be more negative, but it may be that less understood factors such as fertilizer effects or

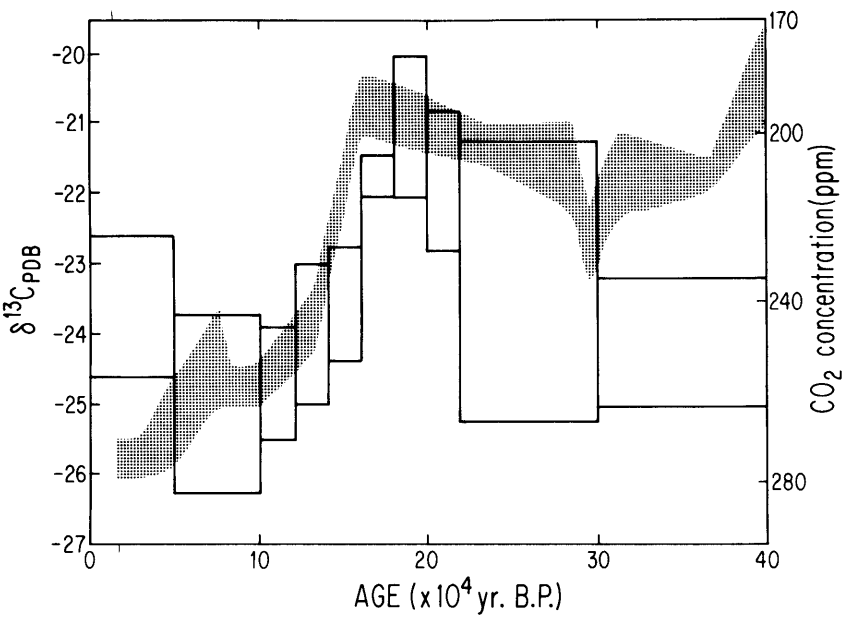

Fig. 3. Mean $\delta^{13}C$ of wood cellulose (all samples) as a function of various time intervals together with the estimated past atmospheric CO_2 fluctuations (shaded area) obtained from air bubbles trapped in ice core. The vertical and horizontal bars on the $\delta^{13}C$ values indicate the standard deviation on the isotopic ratio and dates respectively.

regional volcanism might account for a larger scatter in the $\delta^{13}C$ values of modern samples. On the whole, however, the modern samples are more negative than the glacial samples. This is more obvious from Fig. 2 where the $\delta^{13}C$ values of samples from the same geographic region belonging to different ages are shown. Data in Fig. 2 as well as the fact that we have a relatively large number of data points strengthens our contention that the difference in $\delta^{13}C$ between samples of glacial maximum period and the interglacial period is not due to any species related differences.

Fig. 3 shows that the $\delta^{13}C$ values of the cellulose from wood sampled over a wide geographic range is inversely related to the concentration level of CO_2 taken from the ice core data of Barnola et al. (1987). There have been many attempts to define the factors responsible for the observed $\delta^{13}C$ in plant material (Park and Epstein, 1960; O'Leary, 1981; Francey and Farquhar, 1983). Among the factors suggested to affect the $\delta^{13}C$ of plant materials are the concentration and $\delta^{13}C$ of the atmospheric CO_2, the diffusion characteristics of CO_2 into and out of the leaf walls, the internal concentration of CO_2 inside the leaf intercellular space, efficiency of translocation of "dissolved CO_2" with respect to its enzymatic fixation and finally the step involving the enzyme fixation itself. Climatic factors such as temperature and precipitation may have their own modifying effects, but studies of a quantitative nature related to this are limited.

Park and Epstein (1960) observed that the $\delta^{13}C$ of tomato plants were affected only to a small degree for large variations in CO_2 supply. For a change in CO_2 concentration from 0.05 to 0.015 volume per cent, the $\delta^{13}C$ value of the tomato plants became heavier by 1.6‰. A shift towards a negative value by the same magnitude took place for a CO_2 concentration increase from 0.05 volume per cent to 1.5 volume per cent. The growth rate of the tomato plants, as estimated from the average plant weight responded significantly to the decrease in CO_2 concentration; the yield of fixed carbon dropping by a factor of about 4. The increased CO_2 concentration, on the other hand, did not significantly affect the fixed carbon yield. There are several experiments which indicate a direct response in the photosynthesis rate by plants to changing CO_2 concentrations (Rogers et al., 1983; Rosenberg, 1981; Allen et al., 1987). However, none of these studies deals with the changes in the carbon isotope ratios. Thus, although the above experiment indicated a tendency for plants to be enriched in ^{13}C the observed degree of enrichment falls well below the 4‰ shift observed in our glacial samples, especially considering that the atmospheric CO_2 levels changed by only about 30% between glacial and interglacial periods. In the absence of isotope measurements which suggests large changes in carbon isotope fractionation due to even a relatively large CO_2 concentration changes (Park and Epstein, 1960), other possibilities for the 4‰ change in the glacial-interglacial transition period must be found. We propose two possible mechanisms which individually or in combination may have resulted in the ^{13}C enrichment in the glacial wood cellulose.

4. Causes for the variation in atmospheric CO_2 and $\delta^{13}C$ in glacial wood

There is considerable debate over the factors responsible for a sharp change in atmospheric CO_2 levels between the end of the glacial and the onset of the interglacial periods (Broecker, 1982; Stauffer et al., 1984; Sarmiento and Toggweiler, 1984; McElroy, 1983; Siegenthaler and Wenk, 1984; Mix, 1989). All the theories favour extensive ocean participation as the chief cause and seek to explain the observed 0.5–0.7‰ decrease in the $\delta^{13}C$ of benthic foraminifera belonging to the glacial age and also the proposed productivity changes in the glacial oceans. This shift towards more negative values imply that the $\delta^{13}C$ of the glacial oceanic carbon pool was more negative. The mechanism responsible for this shift may be a transfer of carbon to the oceans by the destruction of part of the terrestrial bio-mass (Shackleton, 1977) or the erosion of shelf-sediments (Broecker, 1982). A shift in the $\delta^{13}C$ of the oceanic carbon pool is also possible via circulation changes in high latitudes (Siegenthaler and Wenk, 1984). However the various models suggested do not fully explain the causes for the glacial-interglacial CO_2 variations (Siegenthaler, 1988). For example, it is generally believed that

the 0.5‰ shift in the oceanic carbon pool during the glacial times can have a large uncertainty in this figure caused by pore-water effects (Broecker and Peng, 1986; McCorkle et al., 1985). The model discussed by Siegenthaler and Wenk (1984) on the other hand predicts the total CO_2 pool of the oceans to be heavier by the same amount. Our study clearly points to processes that could cause a 4‰ change in $\delta^{13}C$ between glacial wood and interglacial wood and hence in the atmospheric CO_2.

One consideration that has received less attention that it deserves is a possible re-arrangement of the terrestrial carbon reservoir during glacial times. This re-arrangement is likely through the formation of vegetation in the vast area of fertile land exposed by the glacially induced lowering of the sea levels. Such a compensation by shelf vegetation for loss of bio-mass in other terrestrial reservoirs due to the ice-caps can be expected to parallel the progress of glaciation reaching the highest in the final phases of glaciation when maximum exposure of the shelf regions took place. In this connection the oxygen isotope and CO_2 record found in the Vostok ice-core (Barnola et al., 1987) can be particularly relevant. Firstly both the $\delta^{18}O$ and CO_2 concentration records exhibit a rather sympathetic variation. Since the variation in $\delta^{18}O$ in the ice core is a measure of the surface air temperature conditions at the site of snow accumulation, the ice-core $\delta^{18}O$ profile documents the progress of glaciation or increase in ice-volume and drop in sea-levels. In other words it can also be looked upon as an index of the increase in the area of exposed land. Secondly, the decrease in the concentration of atmospheric CO_2 appears to be continuous suggesting that equilibration between atmospheric CO_2 and the oceans could not be maintained. This could only be achieved if some process had operated at a rate greater than that required for equilibration between the two reservoirs. One process that we propose is the continuous abstraction of CO_2 by biota growing in the continental margins. Since fixing of CO_2 by plants preferentially incorporates the lighter isotope, a progressive vegetational sink corresponding to the CO_2 drop seen in the ice-core data can cause the atmospheric CO_2 to be progressively enriched in ^{13}C. It should also be noted that the $\delta^{13}C$ value of the atmospheric CO_2 could register large variations without the isotopic composition of the oceanic carbon pool being affected. This arises because the isotopic equilibrium between atmospheric CO_2 and the oceanic dissolved carbon is established at a rate much slower than the chemical equilibrium (Broecker et al., 1980). A shift away from equilibrium fractionations, leaving the $\delta^{13}C$ of glacial atmospheric CO_2 to be enriched in ^{13}C, independent of the oceanic carbon pool could be enhanced by the likely reduced air–sea exchange rates or enhanced biological productivity in the surface waters. The latter process seems to be the explanation for the deviation from the equilibrium values in the $\delta^{13}C$ of atmospheric CO_2 over the oceans today (Kroopnik et al., 1977).

There is growing evidence that the sea surface productivity of the glacial ocean was several times higher than the interglacial ocean (Sarntheim et al., 1988), which should shift the $\delta^{13}C$ of the atmospheric CO_2 further away from the equilibrium value. It is also worth noting that available information on the $\delta^{13}C$ of organic carbon in ocean sediment cores show that the last glacial age organic carbon, presumably produced in the oceanic surface, was 2 to 3‰ heavier than the interglacial counterpart (Sarntheim et al., 1988). Since oceanic organic carbon is produced at the surface, and the atmospheric CO_2 involved in the production of glacial organic matter, this finding is consistent with our contention that the $\delta^{13}C$ of the glacial atmospheric CO_2 was heavier.

A tentative estimate of the efficiency of CO_2 removal by this mechanism can be made as follows. Estimated inventory of carbon in living components of terrestrial ecosystems, excluding the agricultural and urban contributions, is about 5.32×10^{17} g (Emanuel et al., 1981). It is estimated that the last glaciation was accompanied by a lowering of the sea levels by about 150 m. Now given the fact that about 7.6% of the total ocean area of 361×10^6 km^2 falls in the 0–200 m (Menard and Smith, 1966; Duxbury, 1971), a lowering of the sea levels by this amplitude makes available an additional land area of 20×10^6 km^2, which is about 14% of the total land area of 148×10^6 km^2. As a rough approximation, if the newly created land area could initially store carbon in the range of 10 kg/m^2, which is not unreasonable based on the estimated range of 8.6–11.3 kg/m^2 for soil carbon

storage in tropical soils (Schlesinger, 1986), this would account for the storage of as much as 2×10^{17} g carbon. This is equivalent to about 33% of the atmospheric CO_2 concentration of 6×10^{17} g carbon. It is interesting to note that a carbon storage capacity of 20 rather than 10 kg/m^2 for the newly exposed land area will result in a reservoir of 4×10^{17} g carbon. Thus one can see that the land area exposed during low sea levels can in principle abstract significant amounts of CO_2. Evidence of fresh water peat on the continental shelf off north eastern United States and several other areas of the world which are now below the present sea levels lends some support to this scheme (Emery et al., 1967).

If it is plausible that during a glaciation vegetation growing on the newly created landscape can sequester significant quantities of atmospheric CO_2, it follows that the CO_2 concentration changes in the atmosphere observed in the last glacial-interglacial cycle must have taken place during similar climatic events in the past. Two sets of information that help verify this come from the work of Shackleton et al. (1983) and Barnola et al. (1987). The former seeks to estimate atmospheric CO_2 changes from the record of $\delta^{13}C$ in surface and deep water foraminifera in core V19–30 from the equatorial Pacific. Interpretation of this record in terms of past CO_2 fluctuations is, beset with several problems. For instance, as opposed to the mechanism proposed by Broecker in which surface water foraminifera showed little or no change in the $\delta^{13}C$ between glacial and interglacial period, the core V19–30 shows variations in $\delta^{13}C$ similar in magnitude for both surface and deep water foraminifera. Moreover, the surface and deep water records do not appear to be synchronous. The large shift in the $\delta^{13}C$ of U. senticosa (deep water) between 70–60k yr is not evident in the N. dutertrei (surface) record. The ^{18}O record from the same region also fails to reveal any major climatic changes around this time. Obviously, although Shackleton et al.'s work appears to be promising, many more analyses need to be made from several oceanic locations and the factors that affect the $\delta^{13}C$ of foraminifera understood better before translating such records into an atmospheric CO_2 record. The work by Barnola et al., on the other hand, involves the direct measurement of air bubbles in ice cores from Vostok in East Antarctica and does indeed indicate a relatively low CO_2 level associated with the penultimate glaciation as well as a rapid increase associated with the last interglacial, supporting the fluctuations in the concentration of atmospheric CO_2 in response to glacial-interglacial cycles contained in our hypothesis.

The second mechanism that can lead to a ^{13}C enrichment in the glacial wood samples is based on our present understanding of the fractionation during photosynthetic fixation of carbon. We must also point out that since experiments dealing with isotope effects in plants grown under varying CO_2 concentrations are very limited, more work of this nature needs to be carried out to verify this explanation. As shown by O'Leary (1981), Park and Epstein (1960) and Francey and Farquhar (1983), the simplified scheme below depicts the carbon flow during photosynthesis:

$$CO_{2_{\text{atmosphere}}} \rightarrow \text{“dissolved } CO_2\text{”} \rightarrow R{-}CO_2 \text{ (photosynthate).}$$

The δ values of the intermediate species "dissolved CO_2" and subsequently that of the fixed carbon can be greatly influenced depending only on the efficiency of the uptake of gaseous CO_2 by plants, that is step 1. For example if back diffusion of CO_2 is significant, it can cause the "dissolved CO_2" and thus the photosynthate to be heavier. Such a back diffusion under the lower atmospheric CO_2 levels during the glacial period may be the result of an increase in the number of stomatal openings to enhance the efficiency of CO_2 uptake (Woodward, 1987). Additionally, as suggested by Park and Epstein (1960), at low CO_2 concentrations the immediate atmosphere around the leaves may be depleted more efficiently so that some of the local ^{13}C enriched atmospheric CO_2 is incorporated into the plant. In this scenario we start with an atmosphere already lower in its CO_2 concentration whereas the first hypothesis we proposed provides a viable mechanism for the lowering of the glacial atmospheric CO_2 concentration and its effect on the isotopic composition of biota growing at that time.

5. Conclusions

The $\delta^{13}C$ values of wood cellulose belonging to the glacial maximum period (18 ± 2k yr) is about

4‰ heavier than the corresponding ones belonging to the interglacial. Available information on the $\delta^{13}C$ dependency on climatic parameters, especially relative humidity, would call for extraordinarily low humidities for the glacial period. Therefore, this enrichment in ^{13}C could not be entirely due to climatic conditions prevailing at that time, although one cannot rule out a contribution from the general aridity thought to have prevailed during the glacial period. One factor that can affect the $\delta^{13}C$ of glacial wood is a relatively heavier $\delta^{13}C$ of the glacial atmospheric CO_2 that accompanied the lowering of its concentration. There is direct evidence based on ice-core studies for the latter and our results may throw some light on the former. The difference in the $\delta^{13}C$ values between glacial and interglacial wood cellulose, if entirely due to a change in the $\delta^{13}C$ of the respective atmospheric CO_2, the glacial atmospheric CO_2 should have had $\delta^{13}C$ in the range of -3‰. Indeed, our present analysis still has large gaps in time, but the promise held out by these measurements is clearly indicated and should be viewed as a basis for studying the effect of large scale atmospheric CO_2 fluctuations on the biosphere. Similar studies using well-preserved and more accurately dated samples can reduce the scatter in data further and supplement deep sea core and ice-core based studies. Simple calculations show that the land area exposed by the lowering of sea levels can fix significant amounts of CO_2, a possibility that needs to be considered as a potential modulator of atmospheric CO_2.

6. Acknowledgements

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Appendix A. Details of location and age of the wood samples analyzed for their $^{13}C/^{12}C$ ratio

No.	Age (years)	$\delta^{13}C$	Site descriptions
ANU-32	42,130 ± 2,000	−23	Auckland, New Zealand
I-4170	40,000	−24.6	Puerto Vargas, Llanquihue
W2653	36,000 ± 2,000	−23.7	Mt. St. Helens, Washington
UA232	32,000	−25.1	Old Crown Basin, Alaska Creek, Alabama
USGS117	25,500 ± 350	−26.2	Washington
AHA23	25,300 ± 950	−22.5	Gerstle R.; North flank of
ANU33	25,370 ± 300	−20.5	Auckland, New Zealand
W1181	22,400 ± 800	−24.4	West Point, Seattle, Washington
W618	22,200 ± 1,000	−24	Fort Calhoun, Nebraska
W414(51)	22,000 ± 1,000	−21.5	Upper Branch Creek, Ohio
W3944	21,000	−21.2	Georgia
CHI 3	21,000	−20.3	Laguna Bonita, Osorno, Chile
W876	20,600 ± 500	−20.8	Promontory Point, Utah
W1091	20,350 ± 600	−21.6	Seattle, Washington
W877	20,000	−18.9	Little Valley, Utah
W645	19,940 ± 300	−21.1	Yankeetown, Indiana
W2908	19,800 ± 700	−19.4	Lake Bonneville, Utah

No.	Age (years)	$\delta^{13}C$	Site descriptions
W4421	19,700 ± 200	−20.5	Salt Lake City, Utah
W4445	19,580 ± 280	−20.8	Poke's Point, Utah
W879	19,050 ± 300	−22.5	Logan Quarry, Iowa
W4695	18,800 ± 180	−20.2	Salt Lake City, Utah
W520	18,530 ± 500	−20.8	Pleasure Ridge Park, Kentucky
III-1	18,460	−21.4	Spruce from Farmdale, Illinois
W4687	18,000 ± 180	−21.6	Sugar House, Utah
W4327	18,000	−21.1	Hendricks Co., Indiana
W91, 106, 124	18,100	−20.7	Ross Co., Ohio
W470	17,800	−21.8	Bonfiles, Missouri
W113, 126	16,720 ± 600	−21.8	Mitchelville, Iowa
AHA26	15,455 ± 130	−24.6	Willow, N. Bank of Koyukuk R. Southern flank, Brooks Range, Alaska
W1305	15,100 ± 600	−24.7	Seattle, Washington
W153	14,700 ± 400	−23	Story Co., Iowa
W512	14,470 ± 300	−22.5	Greene Co., Iowa
W881	14,300	−22.9	Willow R., Iowa
USGS32	14,300 ± 200	−23.9	Sears Lake, California
ARC33	13,500	−25.5	Brooks R., Alaska
W430	12,920 ± 400	−25.3	Parker'stown, Ohio
W138, 140	12,650 ± 350	−23	Glenwood, Indiana
W1756	12,340 ± 300	−23	Davidson Co., S. Dakota
W58	12,380 ± 360	−23.5	Noble Co., Indiana
W499	12,270	−22.3	Eddy Co., New Mexico
W1824	12,290 ± 350	−23	Roy Co., Utah
AHa24	12,170 ± 270	−25	N. Brooks Range, Alaska
W161	12,200 ± 350	−24.3	Iowa
W498	11,850	−23.5	Eddy Co., New Mexico
TCR-B	11,800	−24.5	Two Creek Forest, Wisconsin
W1411	11,560 ± 300	−23.6	Aithin, Minnesota
W4165	11,560 ± 300	−22.6	Calumet Co., Wisconsin
W940	11,640 ± 275	−24.6	Cedarville, Washington
AHa049	11,560 ± 170	−24.3	John R., South Centralbrooks R., Alaska
Acr31	11,400 ± 160	−24.4	Colville R. Delta, Alaska
Acr29	11,240 ± 160	−25.3	Tepagoruk, Alaska
W391	11,130 ± 600	−24.8	Jackson Co., Wisconsin
Acr28	10,980 ± 80	−25.8	Near Teshekpuk Lake, Alaska
W1411	10,770 ± 300	−25.7	Columbus, New Jersey
W3372	10,640 ± 350	−26	Bay Nat. Monument, Alaska
Acr25	10,670 ± 75	−25	Oumalik Schipp R., Alaska
Acr28	10,700 ± 120	−24.7	Near Teshekpuk Lake, Alaska
Acr24	10,520 ± 140	−25.4	Near Teshekpuk Lake, Alaska
Acr23	10,310 ± 150	−25.2	Ikpikpuk R. Delta, Alaska
Acr22	10,220 ± 150	−23.6	Colville R. Delta, Alaska
W1414	10,230 ± 500	−24.1	Gogebic Co., Michigan
W1376	10,200 ± 300	−24.5	Ano Nuevo Creek, California
W4816	10,120 ± 120	−23.2	Manti, Utah
W1005	10,050 ± 300	−24.6	Thompson, N. Dakota

No.	Age (years)	$\delta^{13}C$	Site descriptions
W965	9,600	−24.6	Spruce, White Pine, Michigan
W1361	9,820 ± 300	−25.9	Traill Co., N. Dakota
W325	9,755 ± 300	−25.4	Delaware Co., Indiana
Acr21	9,840 ± 90	−25.6	Colville R. Delta, Alaska
Ar20	9,670 ± 130	−26.6	Ikpikpuk R., Alaska
USGS163	9,600 ± 85	−25.6	Colville R. Delta, Alaska
Acr19	9,570 ± 90	−25	Kikiakrorak R., Alaska
UGA452	9,480 ± 90	−25.6	Yosemite Nat. Park, California
W750	9,000 ± 250	−24.9	Loup R., Nebraska
Acr15	8,050 ± 130	−25.9	Brooks R., Alaska
Acr10	6,220 ± 115	−25	Itkillik R., Alaska
AHA127	5,370 ± 90	−24.3	Central Brook R., Alaska
Acr8	4,225 ± 90	−25.2	Brooks R., Alaska
UGA604	3,320 ± 85	−23.5	Long Meadow Cr., California
USGS187	3,740 ± 85	−24	Kogosakrak R., Alaska
AHa112	3,230 ± 90	−24.5	Brooks R., Alaska
W4438	2,940 ± 90	−23	Capps Glacier, Alaska
AHa111	2,355 ± 80	−23.6	Brooks R., Alaska
USGS145	2,000 ± 120	−21.1	White Mountain, California
AHa66	1,505 ± 80	−24.4	Brooks R., Alaska
AHa089-77	1,260 ± 80	−23	Spruce, Brooks R., Alaska
USGS51	1,200 ± 60	−24.8	Nushkotik, Alaska
UGA603	710 ± 60	−18.8	Pine, Inyo Nat. Forest, California
USGS213	500 ± 70	−24	Emminar, Alaska
W2933	530 ± 200	−25.4	Cascade R., Washington
W4474	300	−22.6	Icy Bay, Alaska
W2934	110 ± 200	−24.6	Cascade R., Washington
MUA3	120	−24.5	Tasmania, Australia
SN01	120	−21.8	Snowy Mountain, Australia
USGS52	120	−23	Hooper Bay, Alaska
ANZ59	110	−21.5	New Zealand
MNY-BO-7	100	−24	New York
UCI1	100	−21.5	Sequoa National Park, California
ALA3	90	−23.5	Walker Lake, Alaska
UAZ2	80	−21.5	Capetown, S. Africa
AHA-MR1	65	−24.7	S. Brooks R., Alaska
AHA-MR-2	55	−24.5	S. Brooks R., Alaska
AHA-MR-3	50	−24.2	S. Brooks R., Alaska
AHA-MR-4	45	−25.3	Sikikpuk R., Alaska
ALK2	40	−23.1	Fairbanks, Alaska
BRL11	40	−24.6	Georgia
NIC2	30	−23.7	Nicaragua
TX764	25	−23	Houston, Texas
H10	25	−23.5	Houston, Texas
NMK4	20	−24	Kenya, Africa
UBLM2	20	−25.5	Madison, Wisconsin
OPW-DF-1	10	−23	Olympic Penins., Washington

No.	Age (years)	$\delta^{13}C$	Site descriptions
OIO-1	20	−22.3	Amsterdam, Ohio
M.002	10	−23.6	Owensville, Missouri
CH1	10	−24.1	Chicago, Illinois
BC2	10	−26	Columbus, Ohio

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